A NEW GENUS AND SPECIES OF RAT FROM BORNEO (RODENTIA: MURIDAE)

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Abstract. — A new genus and species of arboreal rat from Sabah, *Pithecheirops* otion, is described. It is most closely allied to the Sunda Shelf endemic genus *Pithecheir*, but it differs from this genus in lacking both diagnostic features of the arrangement of the inner ear bones, and the inflation of the auditory bulla.

The fragmented lands of the Sunda Shelf (landmasses and islands from 10°N to 10°S and about 96°E to 120°E that are united by seas shallower than 200 m) formed a single, dry continental landmass or were connected to varying degrees during epochs of low sea levels during the Pleistocene. At least 14 genera and 40 species of native murid rodents are known from this region. Five genera are endemics narrowly restricted to Sundaland (Musser & Newcomb 1983). Over the past two decades the systematics of these and other Asian genera has been clarified in an extensive series of publications by Guy Musser. As a result, it has become relatively easy to recognize new taxa and key morphological features. The Sundanese genus Pithecheir Cuvier, 1838 includes two species, P. melanurus Cuvier, 1838 known only from Java, and P. parvus Kloss, 1916 known only from West (Peninsular) Malaysia. Characters of the genus and species were outlined by Kloss (1916), Muul & Lim (1971), and Musser & Newcomb (1983). In 1991, I collected a rat closely allied to Pithecheir on the island of Borneo. This specimen has several features that warrant distinguishing it within both a new species and genus.

Materials and Methods

Specimens examined are in the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C. Many Asian genera of Muridae were examined for comparison but only the individual specimens of the genus *Pithecheir* are listed: *Pithecheir melanurus* USNM 239661 (1). Java, Born at Museum Buitenzorg, Bogor, locality unknown; *Pithecheir parvus* USNM 488796 to 488819 (24). Malaysia, Selangor, various localities.

Terminology of tooth cusps and cranial features follows Musser & Newcomb (1983) and for the inner ear, Voss (1988) and Carleton (1980). Abbreviations for lengths in text are as follows: HB, head and body; T, tail; HF, hindfoot; E, ear.

Pithecheirops, new genus

Type species.—*Pithecheirops otion*, new species.

Included species. — The type species only. Etymology. — A combination of the Greek suffix -ops, having the appearance of, with the generic name *Pithecheir*, of a genus of Sundaland rats.

Diagnosis. — Morphologically a strongly arboreally-adapted rat with: 1) fur long, dense and soft, body fur extending well onto base of tail; 2) tail robust, slickly naked, and at least partially prehensile; 3) hindfeet broad, with large pads, hallux separated by a gap from other digits, with a claw and toepad expanded medially, forefeet also broad, with large palmar pads, pollux with a broad shiny nail; 4) cranium with no postglenoid vacuity; 5) supraorbital ridges strongly flared; 6) squamoso-mastoid foramen absent; 7) auditory bullae small, with no inflation, such that medial base of bulla has a large exposed contribution from petrosal; 8) inner ear with orbicular apophysis present and manubrium of malleus tipped anteriorly (parallel configuration); 9) pars flaccida present; 10) upper molar M^1 with labial cusps t6 and t9 reduced and joined by an enamel ridge; 11) upper M^2 with labial cusps t3 and t9 absent; 12) first two lower molars (the third lower molar unknown) with chevron-shaped pairs of separated cusps.

Pithecheirops otion, new species

Holotype. – USNM 574500, a juvenile male, collected 21 Sep 1991 by Louise H. Emmons, Field no. LHE 673. A skin with right feet only; a skull; and the entire body, with left feet and organs, in fluid. The top of the head was damaged in the trap, making a large hole in the skin, which is sewn up. The animal was kept alive for a day and during this time the top layer of bone was resorbed from the skull under the wound. The lower right M1 is missing, apparently congenitally. M3 is just beginning to erupt and lies below the level of the gumline. The holotype is the only known specimen.

Type locality.—Malaysia: State of Sabah; Danum Valley Field Centre, 4°58'N, 117°48'E (approximately 75 km W Lahad Datu), elevation about 150 m. About 1 km NE of the field centre by road, and about 500 m NW of the road on a study plot trail.

Habitat. — The holotype was trapped at 1.5 m on top of a large stump in dense viny roadside secondary brush on an abandoned logging road. The forest section had been selectively logged from primary forest in 1989. Primary lowland dipterocarp forest still occurs within 600 m and is the dominant vegetation type of the entire surrounding region.

Etymology.—From the Greek *otion*, little ear, referring to the small auditory bullae.

Diagnosis. – The same as for the genus.

Description. – Because the holotype is a juvenile, pelage and body and cranial pro-

753 rom those

portions can be expected to differ from those of adults. Body measurements: HB = 113, T = 117, HF = 25, E = 15, WT = 36 g. Cranial measurements: total length = 32.2; condylo-basal length = 29.4; least interorbital constriction = 6.0; diastema = 8.4; zygomatic breadth = 16.9; nasals length = 10.8; auditory bulla length = 5.3; alveolar length toothrow 7.3; M^1 length = 3.4; M^1 width = 2.0. Testes abdominal. Head and body covered with long, soft, dense and slightly wavy hair. Hair dull and not glossy, about 1.0 cm at midback, guard hairs to 1.5 cm. Body hair extends prominently onto the tail base for 2.5 cm; legs thickly haired to the wrists and heels (Fig. 1). Ears thickly haired at the base and thinly haired on both surfaces at the tips. Dorsal fur rusty-reddish, slightly paler on sides than midback. Guard hairs with broad brown subterminal bands that impart a dusky cast to red upperparts. Base of dorsal fur dark slate gray sharply demarcated from the paler tips. Underparts whitish, with hair white to the roots. Throat and abdomen faintly tinged pale rusty. Inner forelegs whitish, inner thighs rusty with pale hair base. Forefeet clothed above with pure rusty hairs, hindfeet with darker, more brownish-red hairs except whitish hairs at toetips. Soles of feet and toetips unpigmented. Toes pigmented above and below giving feet a dusky cast. All digits except pollux with curved, sharp claws. Pollux with a broad, shiny nail. Vibrissae dark brown, stiff and robust, the longest reaching the shoulder. Genal and superciliary groups sparse, including but one longer whisker in each. Tail robust, unicolored brown, smooth and slightly shiny, thick at the tip, with scales in narrow, even rings. In life it was at least semi-prehensile, the rat twisted it around branches (Fig. 1) but was not seen to coil it. On the dorsal surface of the tailtip, there seems to be a slightly specialized hairless region of wider scales that could form a gripping surface. The feature is unclear due to wrinkling.

Cranium, viewed dorsally, with wide in-

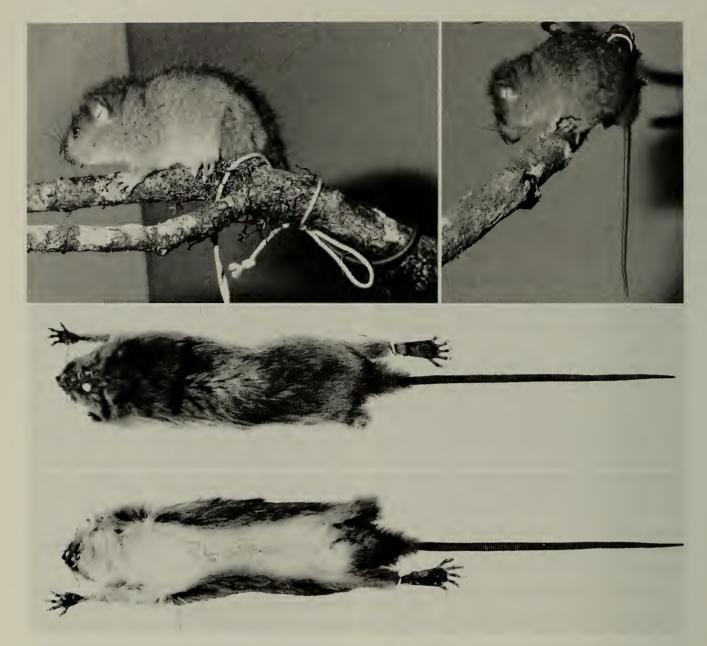


Fig. 1. Pithecheirops otion holotype. Note use of prehensile tail.

terorbital region (Fig. 2); supraorbital ridges strongly flared into shelves; squamosal with a salient point at parietal-frontal suture. Nasals broad anteriorly, tapering only slightly to a straight posterior border. Viewed laterally (Fig. 3), zygomatic arches dip deeply ventrally in a smooth curve, slightly occluding view of the posterior molar. Maxilla deep at its lowest point below jugal. No postglenoid vacuity, auditory bulla solidly fused to squamosal (Fig. 4). No squamosomastoid foramen, but a small indentation in the suture at the place where this foramen would occur (Fig. 4). Ventrally (Fig. 2), auditory bulla tight to the basioccipital, with no medial vacuities except under the eustachian tube. Foramen ovale small (possibly due to youth of the specimen), with no external strut of the alisphenoid (Fig. 4). Posterior opening of alisphenoid canal well anterior to auditory bulla, separated from it by a shelf of bone. Pterygoid fossa shallow, but likely to deepen with age. Incisive foramen reaching to about level of anterior edge of first molar; premaxillary portion of septum within long, about ²/₃ of length of foramen. Posterior palatine foramen slightly posterior to first root of second molar.

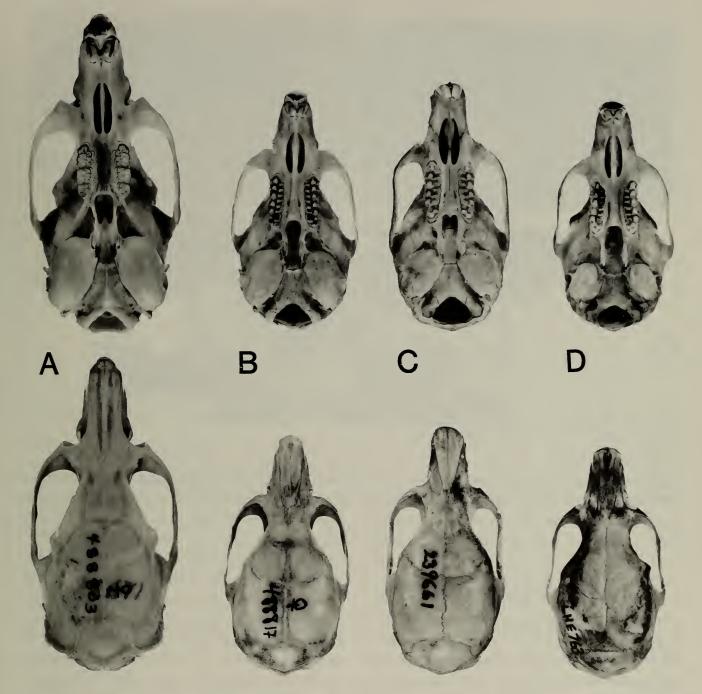


Fig. 2. A) *Pithecheir parvus* adult female USNM 488803; B) *P. parvus* juvenile/subadult USNM 488817; C) *P. melanurus* juvenile USNM 239661; D) *Pithecheirops otion* holotype, juvenile USNM 574500. The juvenile *P. parvus* is older than the *P. otion*, as its third molar is fully erupted. The top of the braincase of D) is damaged from a wound. All photos on each figure are to same scale.

Ectotympanic portion of the auditory bulla not hypertrophied, petrosal exposed. Inner ear with orbicular apophysis present and manubrium of malleus tipped anteriorly (parallel configuration) and pars flaccida present.

Incisors pale orange, almost whitish, approximately orthodont. Lower molars with cusps forming a series of chevron-shaped rows of pairs, labial and lingual cusps separated, of approximately equal size (Fig. 5). Upper molars likewise composed of discretely separated cusps (Fig. 5), a central row of large cusps flanked on either side by rows of smaller cusps. Lingual cusps t1, t4, and t7 of M^1 and M^2 large and of equal size. Large medial cusps t2, t5, and t8 of M^1 , and t2 and t5 of M^2 , also of equal size and spac-

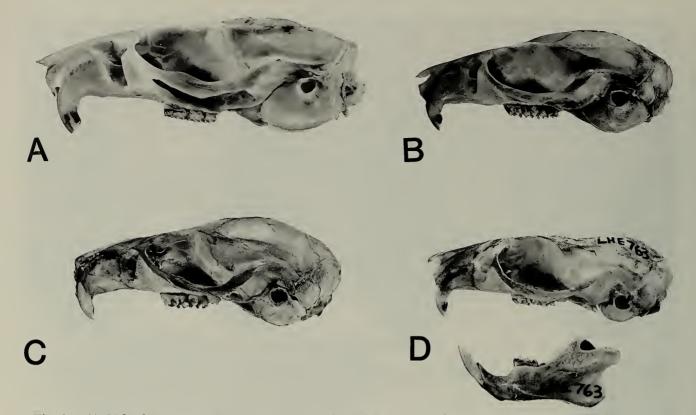


Fig. 3. A) Pithecheir parvus, adult; B) P. parvus juvenile; C) P. melanurus juvenile; D) Pithecheirops otion juvenile holotype. The same specimens as Fig. 2.

ing. On M^1 , t3 widely separated from t6; t6 and t9 reduced, close together, and joined by an enamel crest. T1 bis present as a tiny shelf. On M^2 , t3 and t9 absent and t6 large.

Comparison with Other Species

Musser & Newcomb (1983) compared and discussed many of the characters of *Pithecheir* in relation to other Sundanese genera, and included a hypothesis for the polarity of the characters they define. The following section draws frequently on their work.

Pithecheirops otion shares with Pithecheir spp. characters 1–5 and 12 of the diagnosis, and differs from Pithecheir in characters 6– 11.

Externally, *Pithecheirops otion* is not distinguishable from *Pithecheir* spp. on the basis of the juvenile specimen. The following differences await verification from a series. The hind and forefeet of *Pithecheirops* are dusky above, those of *Pithecheir white* or whitish. The tail of *Pithecheirops otion* seems much shorter: a similar-sized *Pithecheir* parvus (USNM 488796) has head and body length = 122 mm, tail = 157 mm (T = 129%of HB), and a younger one (USNM 488800) 85 mm and 95 mm respectively (112%); versus 113 mm and 117 mm for the Pithecheirops (104%). The mean tail length of adult Pithecheir melanurus (126% of HB) is relatively much longer than that of *P. parvus* (113%, adult measurements from Musser & Newcomb 1983). A prehensile tail is found in no other Sundanese genus but Pithecheir. Two New Guinea rats, Pogonomys and Chiruromys have this derived character. The tail of Pogonomys is hairier distally, and a section of its dorsal tip is hairless and specialized into a gripping surface of broad scales. There is a lesser tendency towards this condition in both Pithecheirops and Pithecheir.

Pithecheirops, like Lenothrix and Pithecheir, has a claw on the hallux, rather than a nail as in the specialized arboreal genera Chiropodomys, Hapalomys, Kadarsonomys and Abditomys (Musser 1982, Musser & Newcomb, 1983). The claw on

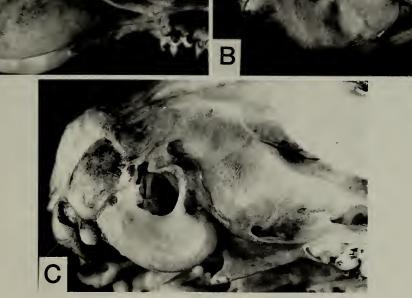


Fig. 4. Region of the auditory bulla A) *Pithecheir parvus* juvenile/subadult; B) *P. melanurus* juvenile; C) *Pithecheirops otion* holotype. The same specimens as in Fig. 2. Note the squamoso-mastoid foramen (arrow) in B), its absence in C); the perpendicular malleus partially visible in A), the ossified area of the pars flaccida in A) and B), and lack of same in C); and the similarity between all crania in the foramen ovale, and postglenoid regions.

the hallux of *P. otion* seems narrower, larger and less modified than that of *Pithecheir*, which is short, with a broad base that shows a tendency toward nailishness (*Pithecheir* was listed as having a nail on the hallux in Musser 1982).

The cranium is similar in size and shape to that of *Pithecheir parvus* of similar dental stage but shorter than one of *P. melanurus* (Figs. 2, 3). The most dramatic difference between the crania of *Pithecheirops* and *Pithecheir* is the lack of inflation of its ectotympanic auditory bulla (Fig. 2). Greatly enlarged bullae are rare among Asian Muridae. Of 14 Sunda Shelf genera, they occur in two others, both arboreal, *Kadarsanomys* and *Hapalomys* (Musser & Newcomb 1983). The exposed wedge of petrosal at the medial base of the auditory bulla in *Pithecheirops* is absent in *Pithecheir*, where it has been suppressed by hypertrophy of the ectotympanic. Consequently, the carotid canal emerges partway down the medial wall of the bulla in the former, but above the base of the bulla in the latter. Likewise, the posterior opening of the alisphenoid canal is well forward of the small bulla of P. otion but crowded right under the anterior edge of the ballooning ectotympanic of Pithecheir spp. Both genera, however, share a general absence or reduction of all vacuities that may surround the base of the auditory bulla, such as in the carotid, alisphenoid, and squamosal regions (Figs. 2, 4). Larger vacuities are present in all other Sundaland genera. Lack of a postglenoid vacuity was deemed the plesiomorphic state by Musser & Newcomb (1983) and Pithecheirops shares this with about half of the Sundanese murid genera.

The perpendicular manubrium and associated lack of orbicular apophysis of the

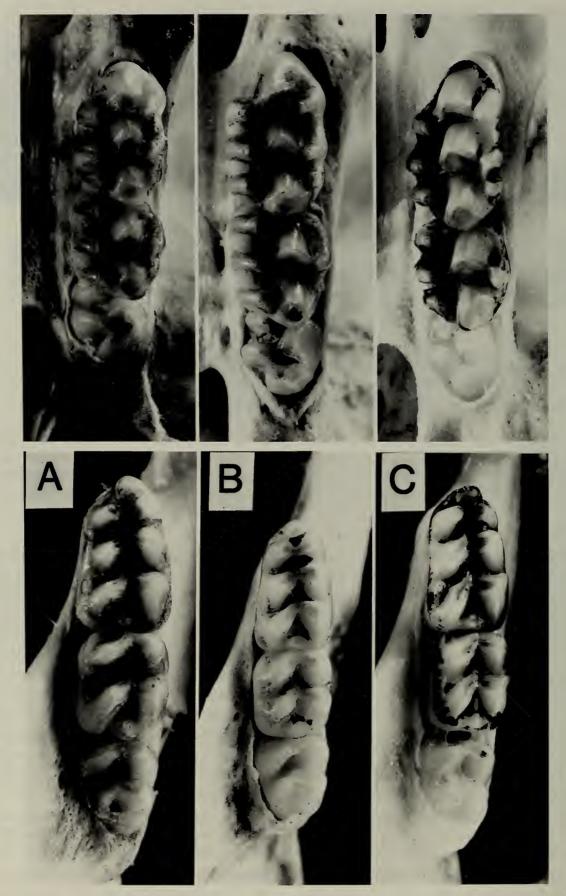


Fig. 5. Upper and lower left toothrows of like-aged individuals of A) *Pithecheir parvus* juvenile USNM 488800; B) *P. melanurus*; and C) *Pithecheirops otion*. B) and C) the same specimens as in Fig. 2.

malleus and the lack of a pars flaccida of the tympanic membrane (see Carleton 1980 and Voss 1988 for discussions of these characters) in *Pithecheir* are features found only in *Hapalomys* among 23 genera of Asian murids examined (see also Carleton & Musser 1984, for other incidences). *Pithecheirops* therefore has the more common condition for these features (pars flaccida present, manubrium of malleus in "parallel" configuration).

A squamoso-mastoid foramen (Fig. 4) is a derived feature present only in *Mus* and *Pithecheir* of Sunda Shelf mice (Musser & Newcomb 1983). It is absent in the holotype of *P. otion*, but there is a suggestion of a notch in the suture where it would occur. In *Pithecheir* the posterior palatine foramen seems more anteriorly positioned than in *Pithecheirops* and the premaxillary portion of the septum in the incisive foramen is shorter.

Pale incisors (should this character prove constant in *P. otion*), is a derived state previously noted only in *Berylmys* among Sundaland murids (Musser & Newcomb 1983).

The upper molars are in general form like those of Pithecheir, but differ in important details. In both species of Pithecheir, cusps t6 and t9 of M¹ are usually well separated by a notch, but as pointed out by Musser & Newcomb (1983) an occasional individual of *P. parvus* shows a tendency for these cusps to join on one or both sides; in P. otion they are connected by an enamel crest. In M² of P. parvus t3 and t9 are prominent nubbins or columns, in P. melanurus t3 seems greatly reduced (only one specimen seen) while t9 is prominent. Both are absent in P. otion. Musser & Newcomb (1983) consider the presence of t3 and t9 to be primitive states, absence of these derived, while presence of t7 is derived. t7 is smaller in P. otion than in Pithecheir spp. The lower molars are similar to those of Pithecheir except the posterior labial cusplet of M₁ is slightly larger, and the anterior labial cusplet slightly smaller.

Discussion of Systematic Relationships

The characters of the genus Pithecheir, apart from a short comment listing three characters supporting specific status of P. melanurus (Muul & Lim 1971), have been discussed recently only by Musser & Newcomb (1983). The teeth were discussed by Misonne (1969). To give a perspective on the relationships of the new genus, it is useful to redefine the genus Pithecheir. The following list includes two characters mentioned by Muul & Lim (1971), those discussed by Musser & Newcomb (1983), Kloss (1916) and some reported here. Because only one subadult cranium of P. melanurus was available for the present study (skin on body in fluid in poor condition), I rely on published measurements and illustrations of that species (Musser & Newcomb 1983).

The genus *Pithecheir* is characterized by: 1) A naked, prehensile tail, scales of the terminal, dorsal 0.5 cm expanded to form a smooth surface; 2) arboreally adapted feet; hallux widely separated from other toes, toepad large, expanded medially, with a claw; 3) ectotympanic of auditory bulla inflated; 4) tympanic membrane with no pars flaccida, this region ossified; 5) malleus with no orbicular apophysis, manubrium perpendicular; 6) squamoso-mastoid foramen present; 7) postglenoid vacuity absent; 8) rows of major cusps on cheek teeth with cusps separate, not fused into laminae in unworn teeth; 9) upper molars with an even row of large, approximately equal-sized lingual cusps t1, t4, t7 on each tooth; 10) labial cusps of upper molars reduced and irregular in size, t6 large, t3 large in M¹, reduced in M^2 , t9 reduced but present in M^1 and M^2 , t6 and t9 of M¹ usually separate in unworn teeth.

Pithecheirops otion is clearly quite closely related to *Pithecheir* by many traits, including both overall appearance, which results from many similarities in features such as texture, color and distribution of the pelage, shape of ears, feet, and body, and appearance of the head and vibrissae. It shares with Pithecheir the derived features of a prehensile tail, flared supraorbital ridges, long incisive foramina, and arrangement of the lingual cusps of the upper molars. It also shares a number of plesiomorphic traits that are nonetheless unusual among Sundanese genera, including absence of a postglenoid vacuity, virtually identical design of the lower molars and central cusps of the upper molars. Pithecheirops does not seem to closely resemble any other genus but Pithecheir. In tooth characters and in lesser inflation of the ectotympanics, Pithecheir melanurus is closer to Pithecheirops otion than is Pithecheir parvus. It is also closer in geographic range.

Of the major characters by which it differs from Pithecheir, and which warrant its placement in a separate genus, the character states in Pithecheirops, including lack of inflated ectotympanic, lack of squamosomastoid foramen, and lack of t3 on M2, are all considered by Musser & Newcomb (1983) to be the less derived conditions. In contrast, the lack of cusps t3 and t9 on the second molar are apomorphic states (Musser & Newcomb 1983). A perpendicular malleus and lack of a pars flaccida are considered by Carleton (1980) to be plesiomorphic, therefore Pithecheirops has the apomorphic condition. However, Voss (1988) argues that the evidence is inconclusive for these two characters, and I here consider the polarity as unknown. Overall, Pithecheirops seems a more primitive relative of Pithecheir, with a few derived traits, but the opposite could be argued. The polarity of the inner-ear characters is the pivotal question.

Of other Asian arboreal rats, only the Indochinese rat *Hapalomys* shares the innerear traits of *Pithecheir*. It also shares a number of derived characters associated with arboreality (and therefore perhaps homoplastic) with both *Pithecheir* and *Pithecheirops*, and some tooth-features (Musser & Newcomb 1983). Among Sunda Shelf genera, *Pithecheirops* seems closer to *Lenothrix* than is *Pithecheir*, because it shares the characters of the auditory apparatus. The polarity of the inner-ear structures is central to determining these relationships. The New Guinea genus *Pogonomys* also shares a mixture of features with *Pithecheirops* and *Lenothrix*. More complete analysis of the relationships of *Pithecheirops* awaits the capture of a good series of specimens.

From the perspective of the characters of all Sunda Shelf rodent genera, Musser & Newcomb (1983:543) concluded that: "On the Sunda Shelf, *Lenothrix* may be closer to *Pithecheir* than to any other Sundanese genera. *Lenothrix*, and even *Pithecheir*, have the aspects of old endemics, relicts left over from an earlier time in the history of the Sunda region and the early evolution of rats there." One can speculate that specialized arboreal habits have allowed the persistence of a number of relict genera in the face of competition from more recent radiations of highly successful advanced rats.

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